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Research article

Colonization and extinction lags drive non-linear responses to warming in mountain plant communities across the Northern Hemisphere

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Global warming is changing plant communities due to the arrival of new species from warmer regions and declining abundance of cold-adapted species. However, experimentally testing predictions about trajectories and rates of community change is challenging because we normally lack an expectation for future community composition, and most warming experiments fail to incorporate colonization by novel species. To address these issues, we analyzed data from 44 whole-community transplant experiments along 22 elevational gradients across the Northern Hemisphere. In these experiments, high-elevation communities were transplanted to lower elevations to simulate warming, while also removing dispersal barriers for lower-elevation species to establish. We quantified the extent and pace at which warmed high-elevation communities shifted towards the taxonomic composition of lower elevation communities. High-elevation plant communities converged towards the composition of low-elevation communities, with higher rates under stronger experimental warming. Strong community shifts occurred in the first year after transplantation then slowed over time, such that communities remained distinct from both origin and destination control by the end of the experimental periods (3-9 years). Changes were driven to a similar extent by both new species colonization and abundance shifts of high-elevation species, but with substantial variation across experiments that could be partly explained by the magnitude and duration of experimental warming, plot size and functional traits. Our macroecological approach reveals that while warmed high-elevation communities increasingly resemble communities at lower elevations today, the slow pace of taxonomic shifts implies considerable colonization and extinction lags, where a novel taxonomic composition of both low- and high-elevation species could coexist for long periods of time. The important contribution of the colonizing species to community change also indicates that once dispersal barriers are overcome, warmed high-elevation communities are vulnerable to encroachment from lower elevation species.

Keywords: Alpine plants, climate warming, elevation gradient, macroecology, transplant experiment, warming experiment

Introduction

Changes in the composition of vegetation along steep elevation gradients reveal the role of climate as a powerful force in structuring plant communities (Giaccone et al. 2019, Chauvier et al. 2021), and now, climate warming is restructuring plant communities (Harrison 2020, IPBES 2023). Climate change effects are especially prominent at higher elevations in mountains, where temperatures are rising faster than the global average (Pepin et al. 2022). The abundance and species composition of mountain plant communities are changing as extant populations respond to new environmental conditions and as species migrate upslope to track their preferred climate (Fig. 1B) (Lenoir et al. 2008, Rumpf et al. 2018). However, vegetation changes are strongly lagging behind expectations based on the pace of climate warming, due to lags in both local extinction (Rumpf et al. 2019) and colonization events (Zu et al. 2021). One expectation is that over time, these lags will be overcome, and high-elevation plant communities will increasingly resemble communities that are currently found at lower elevations (Jurasinski and Kreyling 2007, Savage and Vellend 2015). Alternatively, priority effects and novel plant–plant-climate interactions might set communities on alternative trajectories, yielding 'no-analog' communities, as has occurred under past climatic changes (Overpeck et al. 1992, Leopold et al. 2015, Staples et al. 2022) as well as during current climate warming (Roth et al. 2014). Insight into the trajectory and pace of changes in plant community composition will therefore be important to accurately forecast the impacts of climate change on biodiversity in mountainous regions.

Since both the trajectory and pace of changes in community composition depend on the combined effects of colonization rates, local extinctions, and abundance shifts, we can gain insights into the relative importance of these processes by explicitly examining the response to warming of three distinct species pools (Lynn et al. 2021). Firstly, species that are restricted to high elevation (hereafter 'strictly high-elevation species') are generally expected to respond negatively to warming and eventually become locally extinct (Geppert et al. 2023). This could happen either because they are poorly adapted to warmer conditions, or because they are poorer competitors for resources, such as light, that become increasingly limiting as warm-adapted, lower-elevation species arrive and increase in abundance (Alexander et al. 2015, Olsen et al. 2016). Secondly, species that occur in both high and low-elevation communities (hereafter 'overlapping species'), and thus that are adapted to a wider range of climatic and biotic conditions, might benefit from climate warming and increase in abundance (Lynn et al. 2021). Finally, new species that migrate upslope from low elevation will establish in high-elevation communities and increase in abundance (hereafter 'colonizing species'). The relative contribution of these three local species pools – strictly high-elevation, overlapping and colonizing species – to community shifts in response to climate change will depend on their reaction time (e.g. dispersal, establishment and extinction lags; Alexander et al. 2018) and the magnitude of warming. Disentangling responses of these different species pools can help anticipate the trajectory and rate of changes in high-elevation vegetation and the consequences for species' range shifts under future climate.

Manipulative experiments are key to studying possible long-term changes in community composition in response to climate warming. In situ warming experiments, for example using passive warming chambers, have been most commonly employed to reveal shifts in mountain plant communities towards assemblages more typical of lower elevations (Henry et al. 2022). However, in situ experiments do not capture the contribution of all species pools to community change, most notably that of colonizing species. This is

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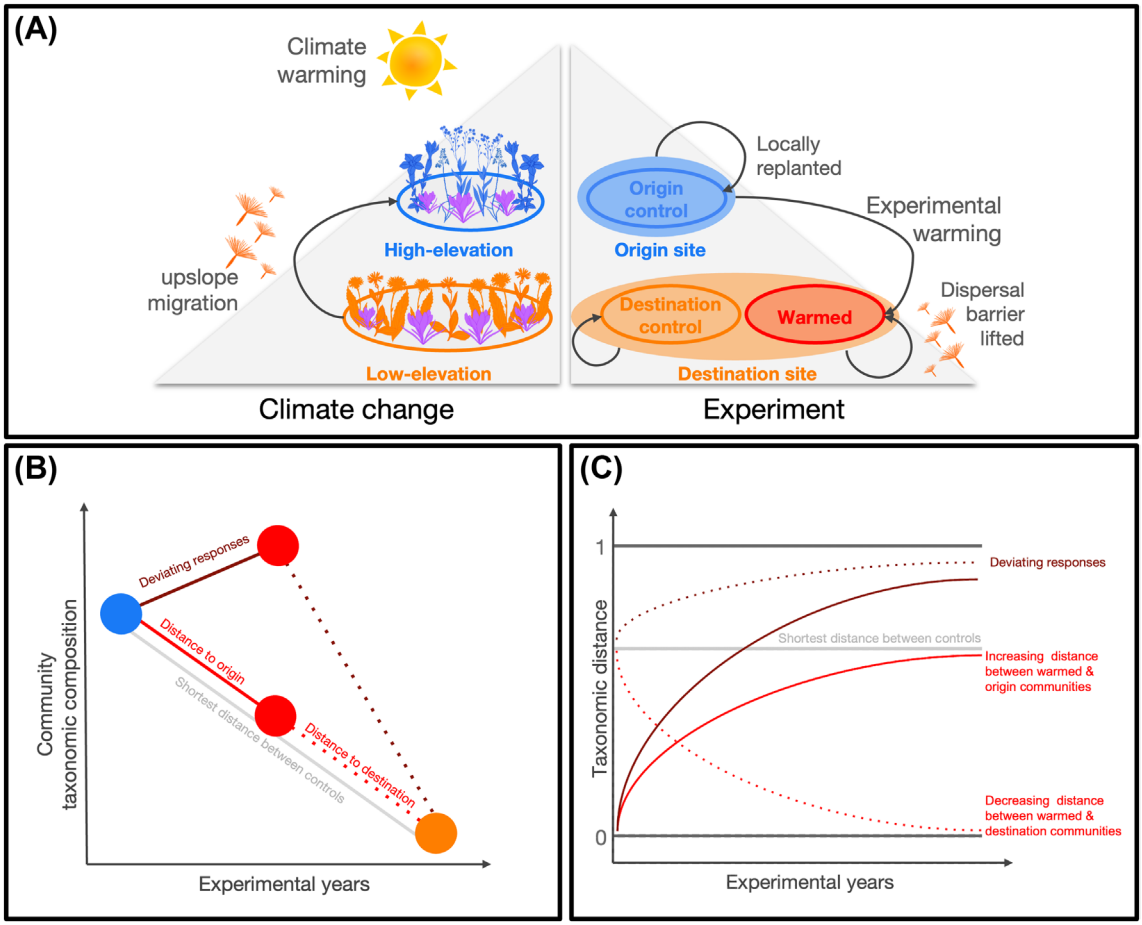

Figure 1. Overview of experimental designs in the TransPlant network, illustrating the ecological processes simulated through whole-community transplantation and the analytical framework used to study community shifts post-transplantation. (A) Transplant experiments aim to simulate climate change by transplanting whole plant communities to putative future climates at lower elevations. This approach also lifts the dispersal barrier for colonizing species, thereby allowing colonization into the transplanted communities from the low-elevation site (colonizing species). We refer to the turfs transplanted from origin to destination sites as 'warmed' communities (red circle), and to turfs locally replanted at origin and destination sites as 'origin' (blue circle) and 'destination' (orange circle) controls, respectively. (B) Our expectation is that the warmed communities (red circle) will diverge in taxonomic composition from the origin controls (blue circle) and increasingly resemble the destination controls (orange circle), following the shortest distance between the controls over the years after transplantation. However, communities might deviate from this expected trajectory of resembling destination controls (red lines), showing deviating responses (pink lines). To quantify the degree of divergence from origin controls (solid lines) or convergence towards destination controls (dotted lines), we calculate the taxonomic distances of warmed communities to either origin or destination controls, respectively. (C) Over the experimental years, we expect that taxonomic distances between warmed and control communities change. If warmed communities follow the expected trajectory (red lines), the distance between warmed and origin control communities will increase (red solid line) and the distance between warmed and destination control communities will decrease (red dotted line). If the distance between warmed communities and origin controls reaches the maximum divergence determined by the distance between the controls, and if the distance to destination controls reduces to zero, indicating maximum convergence, then no lags remain in community shifts. However, warmed communities might deviate from this expected trajectory, increasing the taxonomic distances to both controls (pink lines), thereby maintaining lags in community shifts. Given that distances in warmed communities are constrained between zero and the shortest distance between controls for the expected trajectory, and between zero and one for the deviating trajectory, a logarithmic relationship is expected between experimental years and taxonomic distances. Note that the taxonomic distance between controls is expected to remain constant (gray line).

because the pool of potential colonists is typically absent due to dispersal lags, unless this aspect is intentionally manipulated. Whole-community transplant experiments, which simulate climate change by moving plant communities with their soils to a new location representing possible future climate conditions, overcome this problem by simultaneously exposing communities to a change in climate and potential colonization by species from the destination transplant site (Fig. 1A). Thus, they offer a powerful way to examine the trajectory of mountain plant communities under future climate change and how these trajectories are underlain by different species pools once dispersal barriers are lifted.

Individual transplant experiments have already indicated shifts in species' population dynamics (Töpper et al. 2018),

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relative abundances (Yang et al. 2018, Block et al. 2020, Visakorpi et al. 2022, Niu et al. 2023), colonization and extinction events (Vandvik et al. 2020, Schuchardt et al. 2023a) and community assembly processes (Bektaş et al. 2023). Collectively, these studies suggest that under experimental climate change, transplanted high-elevation communities can restructure quickly and resemble lower-elevation communities. While the magnitude and pace of these shifts remain unknown, species pools driving changes in community composition can be region and experiment-dependent. For example, in a transplant experiment in Norway, transplanted turfs were rapidly colonized by low-elevation species, which negatively impacted high-elevation species within the community through novel competitive interactions (Vandvik et al. 2020) In contrast, in an experiment in France, shifts in relative abundances within the existing communities drove the community reassembly (Bektaş et al. 2023). Furthermore, the functional strategies of individual plant species that benefit from climate change exhibit both general and region-specific responses. For example, taller species become more abundant under experimental warming in experiments from Switzerland (Visakorpi et al. 2022) and Norway (Guittar et al. 2016), where taller species have also lower extinction rates (Lynn et al. 2023). In addition, while species with slow resource acquisition were favored under warming in Switzerland (Visakorpi et al. 2022), species with fast resource acquisition strategies coming from warmer habitats colonized and increased their abundance more in colder sites in Norway (Lynn et al. 2023). These regional differences might arise from variations in limiting resources and how they are impacted by climate change, as well as from differences in the magnitude or duration of the experimental warming (Elmendorf et al. 2012). Consequently, it remains unclear whether we can make general predictions about the trajectory and pace of taxonomic responses to warming, and to what extent context-dependencies can be attributed to regional climatic, ecological or experimental differences.

A macroecological experimental approach (Box 1) can allow us to identify general patterns in community composition change under climate change, while quantifying regional and experimental differences (Alexander et al. 2016). Here, we combine, for the first time, vegetation surveys spanning from 2 to 9 years from a network of 44 whole-community downslope transplant experiments along 22 elevation gradients across the Northern Hemisphere to ask: 1) to what extent does the species composition of warmed high-elevation communities diverge from the non-warmed high-elevation communities and converge towards that of low-elevation communities over time? 2) How do different species pools (strictly high-elevation, overlapping, or low-elevation colonizing species) contribute to divergence or convergence in plant community composition associated with climate change? 3) Is variation in overall rates of community change across experiments, as well as the average contribution of different pools to divergence or convergence, influenced by experimental design, the climate context of the study site, or plant functional trait composition?

Methods

Climate data

We extracted monthly mean daily air temperature (°C) and potential evapotranspiration (PET) (mm) data from the ~1 km resolution CHELSA database (Karger et al. 2021) for each site. We calculated the average summer (June, July, August) temperature and annual PET for each site for each year of the experiment. We averaged the summer temperature and annual PET across all years for each experiment to calculate the origin and destination climates. To estimate the experimental climate warming experienced by warmed turfs, we calculated the average difference between destination and origin sites' summer temperature over the experimental years. Transplantation of turfs from high to low elevation simulated 0.5–11.1°C (average of 3.0°C) of experimental warming across all experiments, covering a range of climate change scenarios generated by the IPCC for the next 50 years (IPCC 2022a). The experiments aimed to simulate warming but other environmental changes, such as in PET, are also imposed by downward transplantation (Fig. 2B). However, due to the high spatio-temporal variability of precipitation, especially in mountainous regions, CHELSA model spatial projections convey more uncertainty than temperature projections (Prein and Gobiet 2017). This uncertainty may prevent us from accurately calculating the differences in PET between closely located origin and destination sites. Therefore, we only analyze the effect of PET at the destination sites rather than the difference between sites.

Plant relative abundances

Vegetation surveys varied in timing, temporal resolution, and duration. Survey methodologies were also diverse, including percent cover estimates of all species in the turfs, point-intercept counts, or species-specific sorting of above-ground biomass. Some surveys did not record non-vascular plant categories, rock or bare soil. Thus, we removed inconsistent cover categories from the dataset and converted vascular plant species cover or count data into relative plant abundances to ensure comparability across experiments. The compiled data ranges from 1 to 9 years, for 60 635 observations of 967 identified species and 92 taxa identified only at genus level. We decomposed these species pools into strictly high-elevation, overlapping or colonizing low-elevation species based on their presence/absence in the control communities for each experiment (Supporting information). By definition, strictly high-elevation species were only found in the higher-elevation origin controls for each experiment, including high-elevation species relative to the experiment. We note that these are not necessarily alpine plants in a biogeographic sense (i.e. species found mainly above the treeline). The colonizing low-elevation species pool includes species that do occur in destination

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Box 1. TransPlant network

TransPlant is a network of 22 elevation gradients, distributed across 20 different mountainous regions of the Northern Hemisphere, where whole plant communities have been transplanted to lower elevations to simulate climate change (Fig. 1, 2, Supporting information). The basic design of the transplant experiments involve the transplantation of vegetation turfs (or 'monoliths') of whole plant communities with their soil from a higher (cooler) to a lower (warmer) elevation site to simulate climate warming ('warmed' treatment) (Fig. 1A). Moving plant communities to lower elevation in this way allows plants from the lower elevation site to quickly colonize transplanted turfs, also simulating the arrival of the novel species into high elevation communities that we expect to arrive following climate warming (Fig. 1A). For any given set of warmed turfs, there are 'origin controls' (high-elevation turfs locally transplanted at their high-elevation site of origin) and 'destination controls' (low-elevation turfs locally transplanted at the low-elevation site of destination) (Fig. 1A). Thus, these controls make it possible to disentangle potential transplantation artifacts from the effects of experimental climate change. Along some TransPlant gradients, multiple experiments are conducted by transplanting the turfs from high- to mid-elevation sites, mid- to low-elevation sites, and high- to low-elevation sites (Supporting information). We refer to a set of warmed, origin and destination control turfs within each gradient as an 'experiment' (Fig. 1A), yielding a total of 40 experiments because 12 gradients were composed of more than two sites (Supporting information). The experiments were established between 2007 and 2017. Each experiment had 3–10 replicates of transplant and control turfs, and in total there were 668 turfs varying in sizes between 0.02and 1 m^2 with a mean size of 0.3 m^2 across the 40 experiments. TransPlant network data and experiment-specific results can be visualized on the dedicated Shiny app: https://billurbektas.shinyapps.io/transplantshiny-1

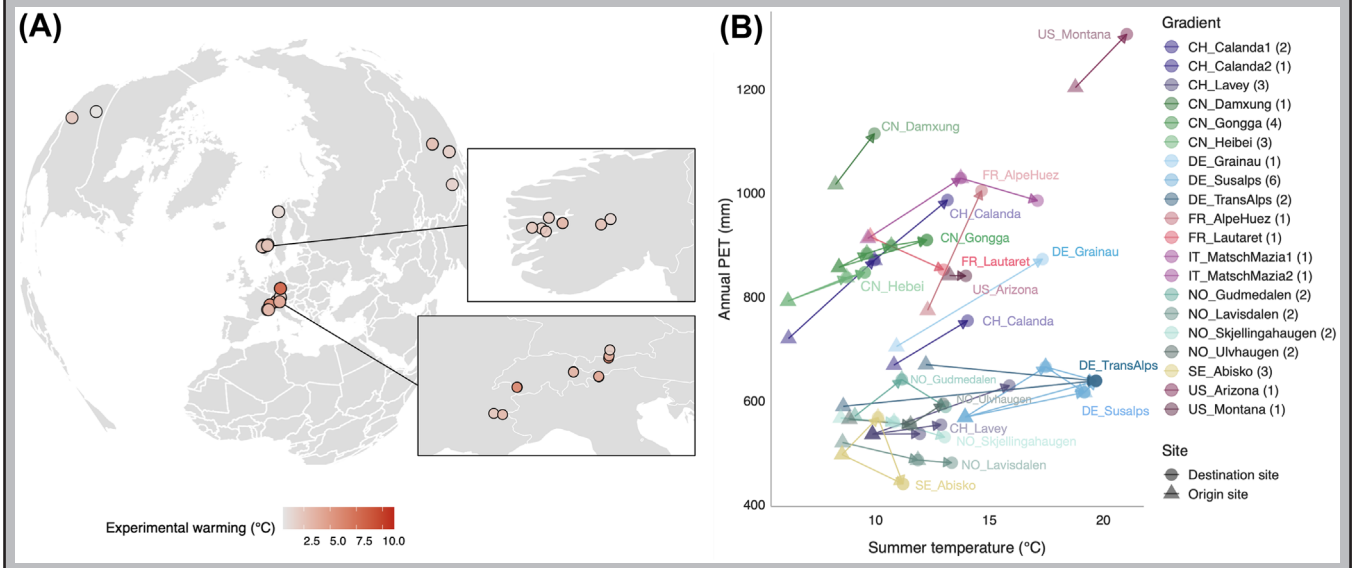

Figure 2. (A) TransPlant experiments across the Northern Hemisphere. The color gradient indicates the magnitude of experimental warming (°C) as the sum of temperature differences between the origin and destination sites across the experimental years. (B) Summer temperature (°C) and annual potential evapotranspiration (PET, mm) of TransPlant sites (circle: destination site, triangle: origin site). Different colors indicate gradients. The number of experiments in each gradient is indicated in the color legend. Coloured arrows indicate the direction of the transplantation for each experiment. Note: We extracted temperature (°C) and PET (mm) from the ~ 1 km resolution CHELSA database for each site (Karger et al. 2021).

controls but not in origin controls. Overlapping species are found both in origin and destination controls. Species that occur in warmed communities only but are absent from both sets of controls (i.e. on average 5% across all experiments, Supporting information) were excluded from the analysis. We limited our analysis to experiments with over two years of data, thus excluding US_Colorado and IN_Kashmir. We also excluded US_Arizona due to its small high-elevation species pool of four species. Additionally, we excluded species found only once in a single turf to eliminate potential botanical identification errors. We square-root transformed species relative abundances in the analyses described below.

Plant functional traits

We compiled five functional traits from the TRY database: vegetative height, leaf area (LA), seed mass, specific leaf area (SLA) and leaf nitrogen percentage (Kattge et al. 2020).

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These traits relate to plant size and resource use strategies that are relevant for plant responses to environmental change and their ability to compete for light, water and nutrients (Violle et al. 2007, Díaz et al. 2016). We used a pre-processed version of the TRY dataset by Walker et al. (2023), filtered for trait values with an error risk < 4 according to the TRY database criterion (which measures the deviation from mean trait values within species, genus, family, or the entire dataset in standard deviation) and gap-filled using Bayesian hierarchical probabilistic matrix factorization imputation. This pre-processed dataset still had missing focal traits for certain species (vegetative height: 22%, SLA: 15%, LA: 31%, N-percent: 23%, seed mass: 29%) that we additionally gap-filled with 'miceRanger' algorithm (Wilson 2021). From these functional traits, we built a principal component analysis (PCA) with all the species from the TransPlant network (Supporting information). Horn's parallel analysis retained two principal components (PC) to represent the variation in the trait space. LA (33%), vegetative height (26%), and seed mass (23%) contributed primarily to PC1, followed by N-percent (9%) and SLA (8%). SLA (42%) and N-percent (38%) contributed the most to PC2, followed by vegetative height (9%), seed mass (9%), and LA (1%). Thus, we defined the first two PCs as denoting plant-size and resource acquisition-related traits, respectively, representing the two main axes of the global plant functional trait spectrum (Díaz et al. 2016). We calculated community-weighted means (CWMs) of PC1 and PC2 scores for each control community, reflecting plant size and resource acquisition strategies, respectively.

Quantifying plant community taxonomic divergence or convergence

To quantify the plant community taxonomic change over time, we built principal response curves (PRC; Van den Brink and Braak 1999). PRC, developed from redundancy analysis (RDA), is an ordination technique that quantifies the impact over time of several treatments on species relative abundances in experimental communities, relative to a reference community. It accounts specifically for the interaction between experimental years and treatment while controlling for the overall temporal trend in community composition. PRC allows for extracting 1) taxonomic distances between the treatments and the reference over time as canonical coefficients of the treatments and 2) species weights that quantify species' contributions to overall community taxonomic changes (Vandvik et al. 2014).

We quantified the taxonomic distances of the warmed communities relative to the controls by constructing two PRCs for each experiment. The first PRC used the origin control as the reference community, with the warmed and destination control as treatments to quantify their taxonomic distance from the origin control. The second PRC used the destination control as the reference, with the warmed and origin control as treatments to quantify their taxonomic distance from the destination control (Supporting information). Canonical coefficients (C_t) from PRC axis 1 (hereafter PRC1) capture the most important taxonomic variation in differences between warmed and control communities for a given year t, quantifying warmed communities' divergence from the origin control and convergence towards the destination control. Canonical coefficients from PRC axis 2 (hereafter PRC2) capture the second most important variation, and most important deviation from the PRC1 (van den Brink et al. 2009). In PRCs, taxonomic distances between the origin and destination controls indicate the maximum expected divergence of warmed communities from origin controls and their maximum expected convergence towards destination controls (Fig. 1B, C). When canonical coefficients of the warmed communities exceed the canonical coefficients of the control communities in a given PRC, this can be interpreted as the communities deviating from the shortest trajectory between warmed communities and displaying a 'deviating' response (Fig. 1B, C). We expect to see these responses mainly in PRC2 with higher values in PRC2 indicating stronger deviating responses.

Quantifying species' contributions to taxonomic divergence or convergence

To assess the species' contributions to the community taxonomic shifts, we calculated proportional relative abundance differences in warmed communities in comparison to the mean relative abundance in control communities following the expression $b_k \times c_t$ for each species k, with species weights b_k and canonical coefficient c_t of warmed communities at year t from both PRCs per experiment. Here, species weights b_k (i.e. constant over the years) allow us to obtain the fitted response curves for species k and quantify the affinity of species k with the overall trajectory of the community (i.e. the higher the species' weights, the more likely it is that the species is aligned with the pattern of community change as quantified by PRC) (Van den Brink and Braak 1999). Interpreting this outcome as the species' contribution to a communities' taxonomic divergence and convergence provides several advantages to using raw relative abundance differences: 1) disentangling species contributions to the most important variation (PRC1) from the second most important variation (PRC2, i.e. deviations from PRC1) community change, while 2) taking into account the noise in the data.

Statistical analyses

To address our first question, we assessed the rate of composition change in warmed communities along two primary axes: 1) divergence or convergence along PRC1, quantified by canonical coefficients, and 2) deviation from these trajectories along PRC2. We developed linear mixed effects models for each axis, considering both the warmed (red lines in Fig. 1B, C) and control communities (gray lines in Fig. 1B, C) relative to a reference community. These models used canonical coefficients as the response variable and included log-transformed experimental year, distance type (to origin or destination control), experiment identity, and their three-way

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interactions as fixed effects. A random effect for gradient was included to adjust for non-independence across experiments due to regional variations like soil and habitat differences. We log-transformed the experimental year to fit a logarithmic regression because the distances between communities cannot surpass the maximum expected distance in the case of the divergence, or zero in the case of convergence. This transformation improved model fit, reducing AIC values by 121.39 and 153.20 for PRC1 and PRC2, respectively (df = 162). The slopes from these models provide estimates of the rates of divergence from origin controls, convergence towards destination controls, and deviations in composition across all experiments over the years.

To answer our second question, we estimated 1) the proportional differences in relative abundances in warmed communities calculated from both PRC axes per species pool (strictly high-elevation, overlapping and colonizing) at the start (year = 1) and end (year = 9, projected for the short experiments) of experiments, and 2) the rate of changes in these proportional differences over time. We built linear mixed effects models for each axis and species pool with species' proportional differences in relative abundances in warmed communities as the response variable with experimental year (log-transformed), comparison type (to origin or destination control), experiment identity, and their three-way interactions as fixed effects. We included species nested in gradients as random effects. Here, we present the estimated proportional differences in relative abundances in warmed communities per species pool at the start and end of experiments, and the slopes (as rate of changes in relative abundances) from these species pool-level models for all experiments combined. When compared to origin controls, higher proportional relative abundance differences in warmed communities indicate greater climate change effects on relative abundances of that experiment and/or species pool. Also compared to origin controls, greater magnitudes of the slopes (absolute values) indicate faster changes in relative abundances. More precisely, higher positive rates indicate faster species gains, while lower negative rates indicate faster losses. When compared to destination controls, 1) higher proportional relative abundance differences in warmed communities indicate greater lags in relative abundances, while 2) larger magnitudes of the slopes (absolute values) indicate faster realization of the experimental climate change response and thus, declines in lags. More precisely, higher positive rates indicate faster decline in colonization lags (i.e. realization of colonization events), and lower negative rates indicate faster decline in extinction lags (i.e. realization of extinction events). Overall, changes in a species pool reflect overall changes in species' relative abundances in a given experimental community belonging to the species pool in question.

To answer our third question, we first extracted the slopes (i.e. rate of changes in distances between warmed and both control communities) and their standard errors for each experiment from the first-mentioned (community-level) model. Second, we extracted the initial and final proportional differences in relative abundances and slopes (i.e. rate of change in proportional differences in relative abundances) and their standard errors for each experiment from the second-mentioned (species pool-level) model. At the community-level, we built two separate meta-regression models to accommodate each of the two distance types (to origin or destination control) with slopes as the response variable. At the species pool-level, we built 18 separate meta-regression models to accommodate each of the two comparison types (to origin or destination control) and three species pools with three response variables: 1) slopes at the species pool-level, 2) initial and 3) final proportional differences in species-pool relative abundances. In these models, experimental (turf size, experimental warming, and duration), climate factors (summer temperature and annual PET of destination sites), and functional traits (CWM of plant size and resource acquisition traits) were included as explanatory variables. Meta-regression models take into account the uncertainty in the response variables (Viechtbauer 2010). All explanatory variables were standardized (i.e. z-score normalization).

We conducted the statistical analysis with R ver. 4.4.0 (www.r-project.org) using the following packages: 'emmeans' (Lenth 2023), 'lme4' (Bates et al. 2015), 'vegan' (Oksanen et al. 2022), 'MuMIn' (Bartoń 2023), 'merTools' (Knowles and Frederick 2024), and 'metafor' (Viechtbauer 2010).

Results

To what extent does the species composition of warmed communities shift over time?

Warmed communities taxonomically diverged from the high-elevation origin control communities (Fig. 3A, red-solid lines; Supporting information) and converged towards low-elevation destination control communities across all experiments (Fig. 3A, red-dotted lines). As expected, the distance between the two control communities remained constant on both PRC axes, indicating no significant directional change in composition in the controls (Fig. 3A, B, gray lines). In the first year, warmed communities had already diverged on PRC1 by on average 14%, and converged by on average 13%, of the maximum expected distance (i.e. the distance between the two controls). If communities maintained this pace they would have reached zero taxonomic distance with destination controls at around seven years, however, rates of divergence and convergence slowed down considerably over time. On average, (i.e. based on projections), 48 and 54% of taxonomic distance on PRC1 still remained, after nine years, for communities to reach maximum divergence and convergence, respectively.

However, variation in rates of composition change was observed across the 40 experiments (Supporting information). First, warming led to divergence from origin controls only in 33 experiments. Conversely, in seven experiments, warmed communities diverged from origin controls in the first year but they started to converge back towards origin

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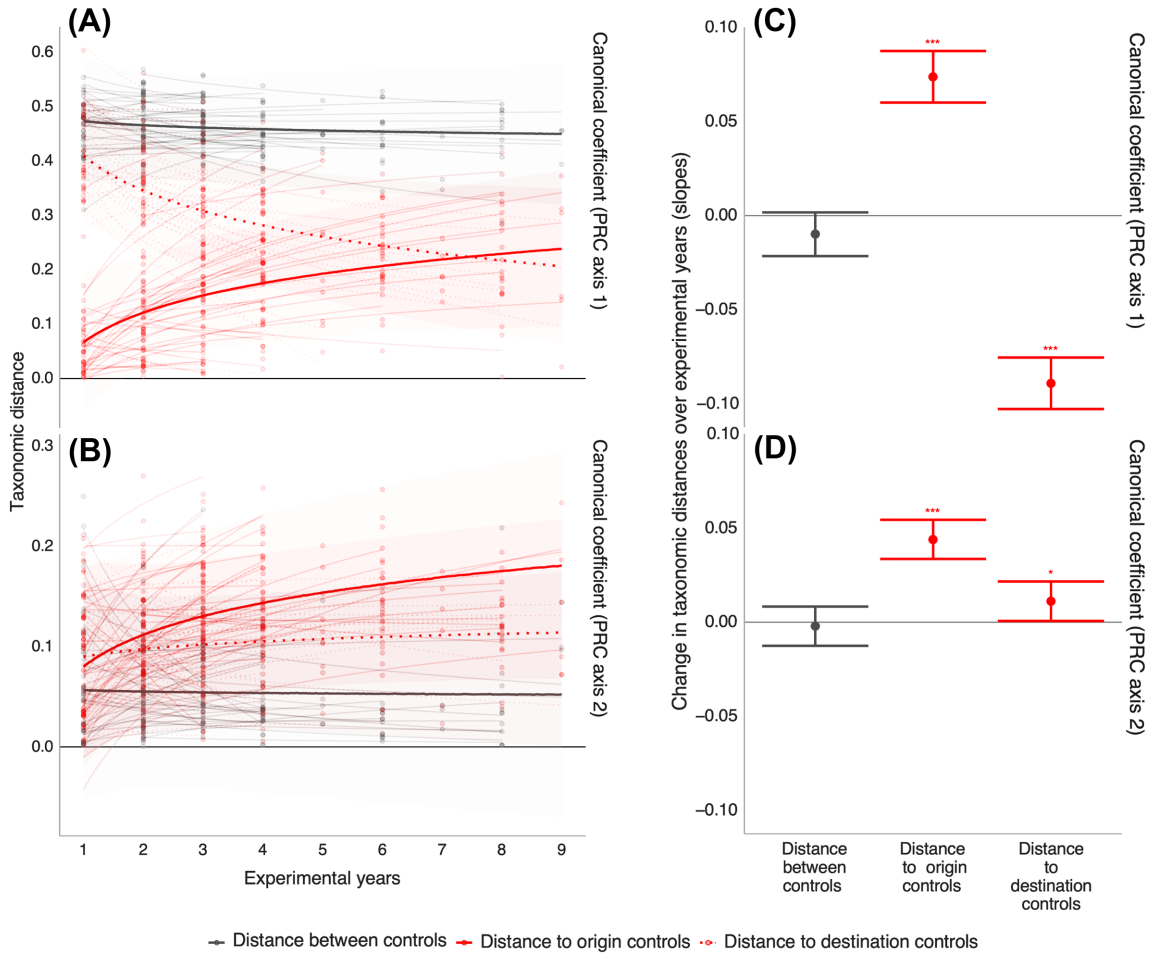

Figure 3. Community divergence and convergence in response to warming, reflected as the change in canonical coefficients reflecting the taxonomic distances between experimental communities and their origin and destination controls over time. (A–B) Each panel reflects both divergence of the warmed community from the origin control (solid lines) and convergence towards the destination control (dotted lines). For divergence, the origin controls are set at zero as the reference community and the plot shows the divergence of warmed communities (solid red line) and destination controls (solid gray line) from the origin controls. For convergence, the destination controls are set at zero and the plot shows the convergence of the warmed communities (dotted red line) and origin controls (solid gray line) towards the destination controls. Distances between controls (gray lines) represent the expected taxonomic distance if warmed communities fully converge (i.e. become identical to the destination community composition). (A) and (B) represent PRC axes 1 and 2, respectively. (C–D) The rate of change in taxonomic distances (i.e. distance per log-transformed experimental year) between control communities and between warmed communities and origin or destination controls, as reflected in the analyses on (A) or (B) where the respective controls are set at zero as the reference community. (C) and (D) represent PRC axes 1 and 2, respectively. Canonical coefficients from PRC1 capture the most important variation in taxonomic distance, and represent the taxonomic divergence from the origin control or convergence towards the destination control due to experimental warming. Canonical coefficients from PRC2 capture the most important deviations from the PRC1, and so represent deviations in the trajectories of the communities as they diverge or converge from/towards origin and destination controls, and thus give deviating responses. Note that lines in (A) and (B) are from models fitted with log-transformed experimental years. Responses of each experiment (fitted separately) and overall responses are shown in thin and thick lines respectively, with shading indicating the 95% confidence interval for the overall effect. In (C) and (D), significant slopes are indicated with *: p. values < 0.05, **: p. values < 0.01, ***: p. values < 0.001.

controls over the years (Fig. 3A, Supporting information). The rates of change in taxonomic distances between warmed and origin control communities ranged from −0.053 to 0.215 (i.e. unitless change in taxonomic distance over the years scaled between −1 and 1, Supporting information). Second, warming led to convergence with destination controls only in 36 experiments. Whereas in four experiments, warmed communities tended to diverge from the destination controls. The rates of change in taxonomic distances between warmed and destination controls ranged from −0.283 to 0.0584. In addition, taxonomic distances between warmed and control communities generally (Fig. 3B, solid and dotted red lines) exceeded the distances between the controls (Fig. 3B, gray lines) along PRC2. This indicates that warmed communities deviated from the expected trajectory of convergence. These deviations significantly increased over time (Fig. 3B, D).

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How do different species pools contribute to divergence or convergence in plant community composition?

The divergence of warmed communities from origin controls was similarly driven by both the decrease in relative abundances of strictly high-elevation species and the increase in colonizing species. (Fig. 4A, B). However, both colonization and extinction lags remained after the nine-year experimental period: on average, strictly high-elevation species remained more abundant and colonizing species less abundant in warmed communities compared to destination controls (Fig. 4A, B). Besides having equal contributions to the overall shifts in warmed communities, rates of species gains and losses over the years were similar, thus contributing equally to the rates of divergence from the origin controls and convergence towards destination controls (Fig. 4C). However, beyond these general trends, there was substantial variation across experiments (Fig. 5A, thin lines; Supporting information). In fact, the relative abundances of overlapping species across experiments showed both increasing and decreasing trends, which canceled each other out, resulting in no clear general trend.

Taxonomic shifts away from the shortest trajectory between origin and destination controls in warmed communities were mainly driven by the colonizing species (Supporting information). Interestingly, when predicted by PRC2, relative abundances of the colonizing species were increasingly higher in warmed communities in comparison to destination controls, indicating that some colonizing species were increasing their abundances more than expected (i.e. given their relative abundances in destination controls), contributing to the community-level deviating responses (Supporting information).

What influences the variation in overall rates of community change across experiments, as well as the contribution of different pools to divergence or convergence?

Communities exposed to stronger warming, over longer periods, in smaller plots and transplanted to drier conditions

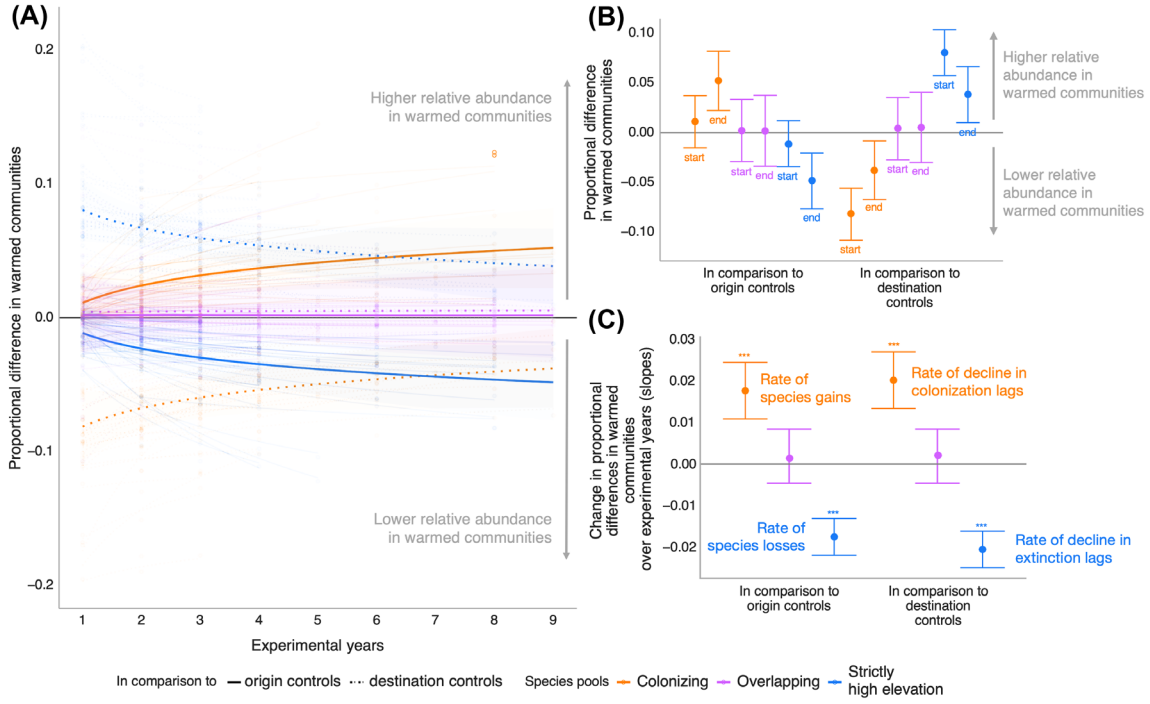

Figure 4. Changes in different species pools in warmed communities in comparison to controls over time. (A) Proportional differences in relative abundances of each species pool in warmed communities in comparison to origin controls (solid lines) and destination controls (dotted lines) calculated from PRC1. Positive values indicate higher relative abundances in warmed communities, negative values indicate lower relative abundances in warmed communities. (B) Predicted proportional differences in relative abundances of different species pools in warmed communities in comparison to controls at the start (year = 1) and end (year = 9, projected for shorter experiments) of the experiments. (C) Rate of changes in proportional differences in warmed communities over log-transformed experimental years. When compared to origin controls, higher positive rates indicate faster species gains, lower negative rates indicate faster losses. When compared to destination controls, higher positive rates indicate faster decline in colonization lags (i.e. realization of colonization events), lower negative rates indicate faster decline in extinction lags (i.e. realization of extinction events). Note that lines in (A) are from models fitted with log-transformed experimental years. Responses of each experiment (fitted separately) and overall responses are shown in thin and thick lines respectively, with shading indicating the 95% confidence interval for the overall effect. In (C), significant slopes are indicated with *: p. values < 0.05, **: p. values < 0.01, ***: p. values < 0.001

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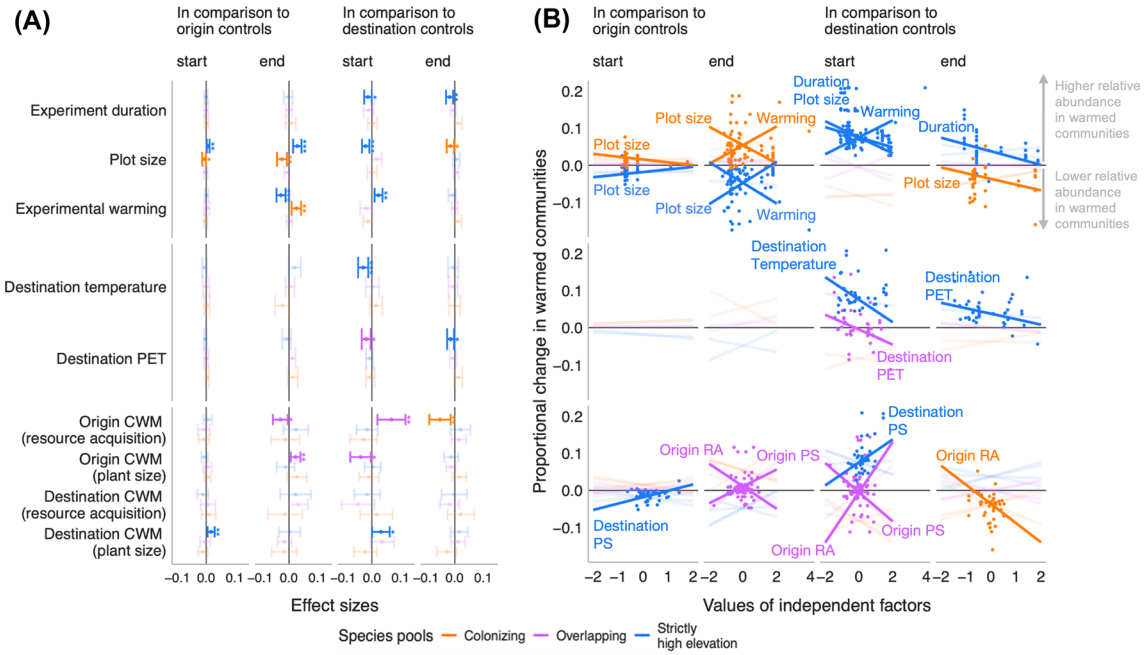

Figure 5. (A) Magnitude of experimental, climatic and functional trait effects on the magnitude of species pool contributions (change in species pools' proportional relative abundance changes in warmed communities in comparison to controls) at the start (year = 1) and end (year = 9, projected for shorter experiments) of the experimental period. (B) Relationships in species pool contributions with experimental, climatic, and functional trait factors. For experimental and climate effects, positive values indicate longer experiment duration, bigger turf sizes, stronger experimental warming, warmer and drier destination site. For functional trait effects, positive values indicate that on average communities are dominated by fast-growing resource-acquisitive (high SLA and leaf nitrogen) and taller species with wider leaves and heavier seeds (Supporting information). When compared to origin controls, positive effect sizes indicate increases in relative abundances in warmed communities with the higher values of the explanatory factor for all species pools. When compared to destination controls, positive effect sizes still indicate higher relative abundances in warmed communities with increasing values of the explanatory factors but it can additionally be interpreted as higher extinction lags for strictly high-elevation species pool with the increasing values of the explanatory factors. For colonizing species, negative effect sizes indicate increasing colonization lags with increasing values of the explanatory factors. In (B), only significant associations as quantified in (A) are shown and labeled. Linear metaregression models were built independently per species pool. All explanatory variables were standardized (i.e. z-score normalization).

diverged faster from origin controls (i.e. increasing taxonomic distances between warmed and origin control communities over time) (Supporting information). Also, communities exposed to stronger warming over longer periods converged faster towards destination controls (i.e. decreasing taxonomic distances between warmed and destination control communities over time) (Supporting information).

Species pools' relative abundance differences in warmed communities compared to controls varied between the beginning and end of experiments (Fig. 5, Supporting information). At the beginning of the experiments, species losses (i.e. decreases in the relative abundances of the strictly high-elevation species) in warmed communities were higher in experiments with smaller plots and when destination communities were dominated by smaller-sized plants. Similarly, extinction lags were greater in smaller plots, under stronger warming, in shorter experiments, when transplanted to cooler destinations where destination communities were dominated with taller-sized plants. Parallely, species gains (i.e. increases in the relative abundances of the colonizing species) in warmed communities were higher in smaller plots. Finally, overlapping species had higher relative abundances in warmed communities in comparison to destination controls when transplanted to a wetter destination (among other destination sites) and when they originated from smaller-sized and more resource-acquisitive communities.

At the end of the experiments, species losses and gains were higher (Fig. 5) and faster (Supporting information) in smaller plots and under stronger warming. Whereas, extinction lags were higher in shorter experiments and when communities were transplanted to wetter conditions. Meanwhile, colonization lags were higher when the origin communities were dominated by more resource-acquisitive strategies. Finally, overlapping species had higher relative abundances in warmed communities than in origin controls when they originated from more conservative and taller-sized communities.

Discussion

High-elevation plant community trajectories under climate warming

Ecologists are trying to understand the reconfigurations of plant communities due to abundance and distribution shifts triggered by climate change. A 'null hypothesis' is that when

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dispersal limitations of warm-adapted species are overcome, the future composition of cool-adapted plant communities converge on the composition of warm-adapted communities of today. Alternatively, altered ecological interactions within warming communities might cause them to exhibit lagged responses or even follow alternative trajectories leading to novel community compositions. A network of transplant experiments provided us with the unique opportunity to examine the initial years of these trajectories under climate warming. As expected, the taxonomic composition of warmed communities shifted, converging towards their lower-elevation communities. Nonetheless, communities under warming did not fully converge on the low-elevation community composition, even up to nine years after transplantation. In addition, we found that warmed communities deviated significantly from the shortest trajectory of community shift between high- and low-elevation sites, and that rates of taxonomic convergence slowed over time. Together, these results suggest that even if high-elevation communities do eventually converge on today's low-elevation community composition, this will be a slow process characterized by significant colonization and extinction lags and transient dynamics leading to a prolonged period of novel community structures (Hastings et al. 2018). Such transient dynamics could be due to demographic lags (Alexander et al. 2018), feedbacks in plant–plant interactions (Alexander et al. 2015, Vandvik et al. 2020, Bektaş et al. 2023), plant-soil nutrient pools (Khedim et al. 2022), or plant–microbial interactions (Zhang et al. 2014).

Taxonomic changes were already large in the first year after transplantation. This might be an effect of the transplantation method, whereby the communities are exposed to an abrupt environmental change. Indeed, community responses to gradual warming might differ from those of abrupt climate manipulations, partly because individual species differ in their demographic responses to fast versus slow warming altering the network of plant–plant interactions (Block et al. 2022). Nonetheless, the rapid responses to more intense warming and drying emphasize the crucial role of extreme events in driving community changes, triggering the loss of less resilient high-elevation species and facilitating swift colonizations by warm-adapted taxa. Even as taxonomic shifts appear to slow down over time, and warmed high-elevation communities stabilize, their vulnerability to extreme climatic events could further accelerate the rate of taxonomic changes, inducing a second wave of abrupt shifts. In fact, in transplant experiments in Switzerland and Austria, colonization of the low-elevation species started only three years after the transplantation, specifically after the drought in 2018, which led to significant species losses in transplanted high-elevation communities (Schuchardt et al. 2023b). With intense heatwaves and droughts becoming more common in mountainous areas (IPCC 2022b), high-elevation communities may undergo multiple swift taxonomic changes, as evidenced by landscape-scale alterations following recent extreme events in the European Alps (Choler 2023).

Contributions of different species pools to changes in community composition

Changes in community composition under warming were influenced both by colonizing species from the destination site and abundance shifts, including local extinctions, of strictly high-elevation species. On average, species gains from colonizing pools and losses from strictly high-elevation species pools, along with the rates of these changes, were of similar magnitude, albeit in opposite directions. This suggests that these two species pools contributed similarly to community changes. The large contributions of the strictly high-elevation species pool to the divergence of warmed communities from the high-elevation communities indicate that even after the first year of transplantation, decreasing relative abundances and local extinction events of cold-adapted species under warming were important. A minority of experiments (n = 5) displayed increasing relative abundance of this species pool over the years, which might be explained by a few species initially tolerating (or even benefiting from) climate change and/or altered plant-plant interactions under warming (Nomoto and Alexander 2021). Fewer losses from this species pool were detected in studies with shorter experimental durations. In longer-term experiments, despite overall losses, the strictly high-elevation species maintained enough abundance to significantly differentiate the warmed community from the destination controls even after nearly a decade. In other words, many of these species appear able to persist for considerable periods of time under significant future warming. This is consistent with estimates of substantial extinction lags in alpine plant communities, especially when species continue to coexist with their original plant community via competition (Rumpf et al. 2019).

Colonizing species also made large contributions to the difference in community composition between warmed and high-elevation communities over time, even though with substantial delays. This clearly demonstrates that under climate change, low-elevation species can colonize high-elevation plant communities if dispersal limitations are removed. This gives a first indication that the lags in range shifts observed in mountain floras (Rumpf et al. 2018, 2019) are at least partly explained by dispersal limitation, and that novel plant establishment should be expected once these limitations are overcome. Moreover, increasing colonizations in smaller plots, which have more exposure to the surrounding colonizing community at the edges due to a larger edge length ratio (e.g. 16 and 4 for 0.0625- and 1-m^2 plots, respectively), contradicts the expectation of colonist establishment from seeds, where larger plots should accommodate a higher probability of dispersal events. This implies that clonal growth may be a key factor facilitating the local expansion of low-elevation species once dispersal lags are overcome (Guittar et al. 2016, Töpper et al. 2018). However, persisting colonization lags in our experiments even after almost a decade demonstrate that establishment lags play also a role in range shift dynamics, perhaps through plant–plant interactions within high-elevation communities (Meineri et al. 2020, Lyu and Alexander

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2022). Thus, future studies should explicitly investigate the biotic interactions between different species pools and their effects on plant demographic cycles.

Overlapping species' contributions to community shifts were highly variable but on average close to zero. This does not imply that species in this pool were unaffected by warming. Instead, it suggests a spectrum of positive and negative responses across and within experiments: the overlapping species pool in each experiment contained a mixture of 'winner' and 'loser' species. Given that overlapping species demonstrate a larger niche in tolerating a broader range of environmental and biotic conditions across elevations, their abundance change in the beginning of experiments may be stochastic. However, if originating from more resource-conservative communities, relative abundances of overlapping species increased more. Moreover, when in drier conditions than all other destinations, their relative abundances were lower than in destination controls. This indicates that responses to drought play a major role in mountain plant population dynamics and drought-tolerant species can be the winners of climate change in the mountains (Visakorpi et al. 2022).

Variation in responses across and within experiments due to biotic interactions?

The large variation in magnitude and direction of species' relative abundance changes, even within the same pool, is typical for the species-level responses to climate change (Rumpf et al. 2018, Töpper et al. 2018). Only partly related to experimental design choices (e.g. plot size, duration and climate context), much of the variation in species responses could be explained by destination or origin communities' functional traits. These traits, which indicate competitive abilities for acquiring light, water and nutrients, suggest that plant–plant interactions and their temporal dynamics may play a role in the observed variation in population dynamics (Lynn et al. 2019, Meineri et al. 2020). For example, colonization lags persisted in warmed communities where resource-acquisitive plants were originally dominating. Perhaps, when high-elevation communities are competitive for resources such as soil nutrients and water, colonizers fail to establish. Moreover, we expected that warmed communities suffering competitive exclusion due to taller surrounding destination communities (Supporting information). Yet, in destination sites dominated by taller-sized plants, species losses were lower and extinction lags were higher. This might suggest that biotic interactions between destination communities and strictly high-elevation species influence the population dynamics of the latter, possibly through tall and wide-leaved destination-species creating shade and thus, cooler microhabitats for intensely warmed high-elevation species. Finally, the effects of functional traits were not consistent across the experimental period and they did not determine the rates of changes in communities and species contributions. This could indicate, on the one hand, initial stochastic losses and gains, on the other hand, plant–plant interactions needing time to adjust, being transient and leading to inconsistencies through feedback between them.

Conclusions and perspectives

Our study underscores the dynamic shifts in high-elevation plant communities due to experimental climate warming, suggesting the formation and persistence of novel communities that complicate future predictions. While community taxonomic convergence towards lower elevations hints at a predictable trajectory under climate change, significant uncertainties due to local factors like climate and initial community composition highlight the need for localized studies. Future research should focus on the variability in temporal and spatial dynamics and investigate the causes of shifts in populations and communities, including the changes in biotic interactions. We encourage expanded collaborative macroecological experiments across diverse ecosystems to better understand plant community responses to climate change.

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Data availability statement

Raw and processed data are archived at Open Science Framework (OSF) under the following link https://doi.org/10.17605/OSF.IO/9874T

Code to clean the raw data is available at: https://doi.org/10.5281/zenodo.13936006

Code to reproduce the analysis is available at: https://doi.org/10.5281/zenodo.13935181

TransPlant Network data and experiment-specific results can be visualized on the dedicated Shiny app: https://billur-bektas.shinyapps.io/transplantshiny-1/ (Chisholm et al. 2024)

Supporting information

The Supporting information associated with this article is available with the online version.

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